

Flocs, flows, and mechanisms decoupling larval supply from settlement

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Abstract

Larval supply, settlement (24 h), and recruitment were measured simultaneously with flow and flocculated particulates (flocs) in a muddy, coastal embayment. Fortuitous observations indicated that flocs drifting above the bed touched down at slack tide. Unexpectedly, results showed that larval supply did not portend settlement for the two most abundant polychaetes, *Mediomastus ambiseta* (resident mud dweller) and *Sabellaria vulgaris* (nonresident sand dweller). Both variables fluctuated widely and were decoupled. Colonization of mud vs. sand trays was not significantly different, also due to high variances. A statistical power analysis indicated that resolving selectivity would require 45 (median) paired, replicate treatments. Time series of near-bed planktonic larvae showed sizeable and sporadic spikes. Even 24-h means failed to predict settlement. *Sabellaria* was numerous in zooplankton pump collections, rare in trays, and nonexistent in ambient sediments. In contrast, *Mediomastus* was absent from pump samples, but dominated mud trays and bottom cores. Floc contents, however, lend insight into these distributions. Densities (of order 10^5 m^{-3}) of *Sabellaria* and *Mediomastus* in flocs greatly exceeded those in tray and pump samples (of order 10^3 m^{-3}). Located between the water column and seafloor, organic-rich flocs may offer transient larvae food, shelter, transport, and perusal of settlement sites. When aggregates touch down, entrained *Mediomastus* might exit upon contact with suitable ambient sediments, whereas nonresident *Sabellaria* remain suspended. Flocs may thus play a critical role in shaping connectivity and structuring species distributions.

Planktonic larvae of some benthic invertebrates actively choose their settlement sites under select field conditions. The pervasiveness of active selection, and the flow regimes in which it occurs, are, however, largely unknown. Habitat colonization by larvae can establish and/or maintain populations, creating dispersion patterns that form templates for higher-order interactions (Zimmer et al. 2009). Historically, studies on settlement, recruitment, and adult distributions have far outnumbered investigations involving larval supply (Ólafsson et al. 1994; Jenkins 2006). Moreover, literature that links supply and settlement is dominated by studies of barnacles and other species settling in the rocky intertidal. Determining the generality of these results requires more research on species from other ecologically important habitats, for example, soft sediments in coastal embayments, marshes, and estuaries.

Investigations on the mechanisms that connect populations are critical for a basic understanding of population dynamics, and for addressing important applied problems, such as how to design marine reserves (Cowen and Sponaugle 2009). Yet, surprisingly few studies have quantified both supply and settlement adequately and simultaneously. Most field research has measured “recruitment”—which is not a life stage and is defined by a sampling method—instead of “settlement,” which is the life stage where larvae touch down on a substrate, metamorphose, and begin a benthic existence. Only “competent” larvae are physiologically capable of settlement and metamorphosis,

but identifying competency is often difficult, and its timing may change with temperature (Zimmerman and Pechenik 1991) and food (Pechenik et al. 1996). Quantifying settlement likewise is notoriously difficult, requiring very short sampling intervals to avoid confounding effects of predation, competition, redistribution, or mortality after touch down.

“Larval supply” or “availability” generally refers to the throng of larvae that potentially reach a targeted substratum. The supply domain may be difficult to identify and can fluctuate with flow. Measuring larval supply has been technology limited (Levin 1990). Collecting frequent, concurrent plankton samples at multiple locations is challenging, especially in high-energy coastal environments (Garland et al. 2002). Methodological deficiencies can invalidate purported predictive relationships between supply and settlement. *Decoupling* of these parameters, and the consequences for population dynamics, may not be as rare as once it seemed (Pineda et al. 2010).

The hydrodynamic context for studies of larval supply and settlement is the bottom boundary-layer flow regime (Nowell and Jumars 1984). Larvae sink passively or swim down while transported and mixed by the flow, eventually hitting bottom. Dynamic scaling between field and laboratory environments, as well as measuring relevant physical variables, in ecological field studies, have been emphasized for decades (Nowell and Jumars 1987), but have proven arduous in practice (Zimmer and Zimmer 2008).

This field study explored mechanisms that may associate larval supply with settlement onto muddy sediments in a shallow coastal embayment. In so doing, we also tested larval settlement choice between mud and sand. Site-specific

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measurements of the near-bed flow regime revealed the local hydrodynamic setting, and allowed direct comparisons between larval concentration and flow speed at the same time and space scales. In addition, flocculated particulates (flocs) were collected when they settled at slack tide. As a result of this research, flocs have emerged as a compelling resource for settlers—potentially providing food, shelter, transport, and perusal of touch-down sites—and as a factor that could shed additional light on observed decoupling of settlement from supply.

Methods

Study site and flow measurements—This study was conducted at “Sta. 35” (41°37.8'N, 70°40.5'W, 14-m depth), an offshore control site for the West Falmouth oil spill study (Sanders et al. 1980), on the northeastern shore of Buzzards Bay, Massachusetts. Sediment is moderately well to poorly sorted sand, covered by 1–2 cm of organic-rich mud ($\geq 70\% < 63 \mu\text{m}$) (Sanders et al. 1980; Butman 1989). Here, Sta. 35 is referred to as a “muddy” site because larvae settle onto the surface facade. The site was selected because the dominant, tidal flow is strongly bidirectional, and wind-driven flows can be weak during late-summer and early-fall season when invertebrate larvae are most abundant (Signell 1987; B. Butman et al. 1988; Sankaranarayanan 2007). There are also accessible historical data on infaunal densities, species diversities, and sediment characteristics for this site (Sanders et al. 1980; Butman 1989).

The 40-km-long, semi-enclosed bay is oriented roughly northeast–southwest. The site was located in the 10-km-wide upper portion, which tilts westward. Tidal forcing from the southern New England shelf (flooding tide from the southwest) reflects off the head of the bay, creating a standing-wave response. In the upper bay, the tidal ellipse is rectilinear, with a mean flow of order 10 cm s^{-1} , oriented along the main axis. In this study, experimental deployments and sampling (over 24 h) were timed to avoid periods of wind-driven flows.

The field layout included an array of sediment trays; a moored, automated, time-series zooplankton pump; and an S4 electromagnetic current meter. Within the maneuvering constraints of the 13-m coastal research vessel (R/V *Asterias*), the tray array, pump, and current meter were deployed along a line normal (northwest–southeast) to the main axis current (northeast–southwest). All collectors and sensors thus would contact the major axis tidal current simultaneously. The array, pump, and current meter were also separated sufficient distances cross-stream to minimize hydrodynamic interactions between them. The pump tripod, the largest structure, was intentionally located on the western end of the instrumented area, about 13 m from the current-meter mooring. The S4 was mounted 1 m above bottom (mab) and 7 m southwest of the trays so that eddies shed from the sphere would not disturb the array.

Data from the current records were used to characterize the advective flow fields during the three deployment intervals (23–24 August, 30–31 August, and 06–07 September 1995) and for correlations with plankton pump results.

The S4 sampled at 1-min intervals between 03 August and 08 September. Velocities were corrected to degrees true and averaged over 5 min (pump sampling interval) or 10 min (velocity time series). The pump and S4 thus collected data within meters of each other and integrated over the same time scales.

Sediment-tray array—Settlement was quantified in trays of defaunated sediment that were buried flush with the seafloor. A relatively short (24 h) deployment interval was selected to minimize effects of post-settlement processes. Once deployed, the disk-shaped trays were flush with the sea floor. Each circular (60-cm diameter) Delrin plastic tray contained a central, removable cup recessed in the top, and a steel plate bolted underneath. The tray sloped ~ 5 degrees from center to periphery, terminating in a razor-thin circumferential edge designed to slide into surrounding sediments. To discourage macrofaunal predators or disturbers, the sediment in each cup (2-cm depth \times 10-cm diameter) was covered by a 1-mm-mesh screen that was flush with sediments. A central vertical rod was connected to the metal plate at one end and a large screw at the other. Using a T-shaped bracket temporarily bolted (holes plugged after bracket removed) into the top of the disk, the tray was twisted into the sediment until it was approximately two-thirds buried and the exposed tray surface was flush with the bed. From above, an ~ 5 -cm-wide annulus of Delrin plastic was visible around the cup.

The two surficial sediment types used in tray experiments were organic-rich mud from Sta. 35, and a low-organic fine sand ($28.7\% < 63 \mu\text{m}$) collected just off the Weepeket Islands (41°37.9'N, 70°40.7'W), about 18 km south of Sta. 35. Three replicates of each treatment were randomly distributed within a 150-m² area; adjacent collectors were < 5 m apart. Van Veen grabs (10 per site) sampled sediments from both locations on the same day. From each grab sample, the top 1–2 cm was carefully removed, pushed through a 1-mm sieve, and frozen (thawed before use). After a 24-h deployment, cup contents were preserved immediately in 80% buffered ethanol with rose bengal stain, and sieved through nested 100- and 500- μm screens.

As a measure of recruitment, sediment cores (10-cm diameter) were taken following cup collections on 24 August (two cores), 31 August (three cores), and 06 September (two cores). The top 2 cm of sediment were preserved in 80% buffered ethanol with rose bengal stain, and later sieved through nested 1000-, 500-, and 100- μm screens.

Flocs—Beginning in early August, scuba divers observed a discontinuous layer of fluffy aggregates (flocs) on the bottom during a rare dive with good visibility at slack water. (Aggregates drifted quickly across the array during ebb and flood tides, making them less noticeable.) Divers sampled the visible floc veneer during each of the three tray deployments with a 60-mL syringe (trimmed tip). Flocs were removed only from the halo region of the tray surface to avoid entrainment of settlers on adjacent sediments. These syringe samples were taken from the surfaces of randomly selected trays just before the cups were retrieved. Floc occupants were quantified from four syringes on 24

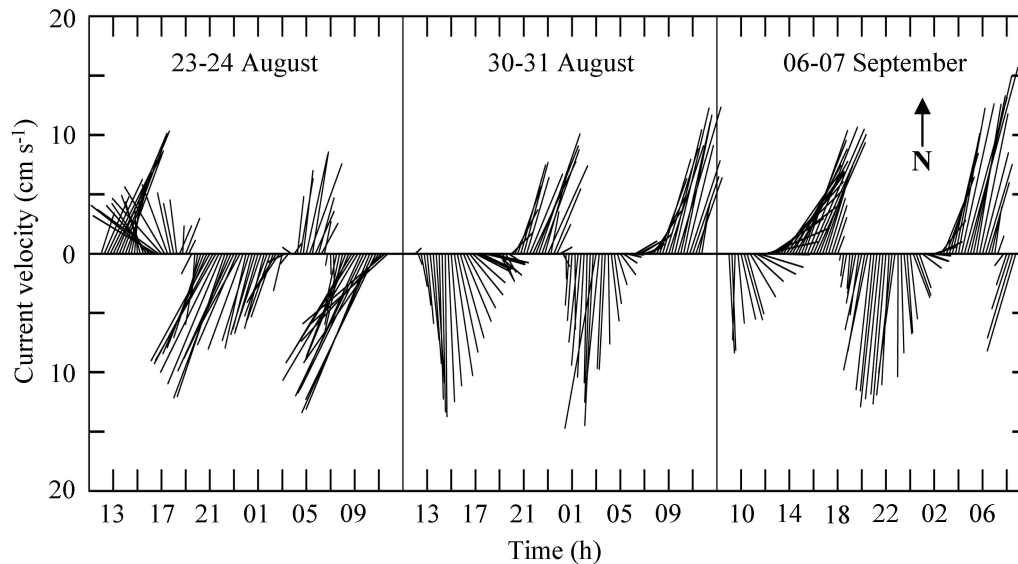


Fig. 1. Velocity time series at Sta. 35 for the three deployment intervals. Plotted are low-passed 10-min averages. Flood current is from the southwest, into Buzzards Bay.

August, two on 31 August, and five on 07 September. Samples were fixed in 4% buffered formaldehyde, and later transferred to 80% buffered ethanol with rose bengal stain.

Plankton pump—Larvae were collected 1 m above the seafloor using a bottom-moored, time-series zooplankton pump, the “Moored, Automated, Serial, Zooplankton Pump” (Doherty and Butman 1990). Autonomous, with computer-controlled sampling, larvae are preserved in situ. At 1 mab, polychaete larvae sinking or swimming downward at $\sim 0.1 \text{ cm s}^{-1}$ (Butman 1989; Tamburri and Zimmer-Faust 1996) would fall to the bed in ~ 15 min, while transported 100–150 m by a $10\text{--}15 \text{ cm s}^{-1}$ current. These distances are well within the scale ($\sim 1 \text{ km}$) of sediment patchiness in this region of Buzzards Bay (Sanders et al. 1980). Therefore, from 1 mab, the pump sampled larvae that, if competent, were available for settling in sediments typifying Sta. 35.

The pump was designed to minimize flow disturbances that may bias collections (Doherty and Butman 1990). These goals were achieved, as indicated by dynamically scaled flume studies (J.D. Sisson and C.A. Zimmer unpubl. data) and by field experiments where pump collections were compared with synchronous samples from a Multiple Opening Closing Net and Experimental Sensing System (0.25-m^2 mouth opening; Wiebe et al. 1985) (C.A. Zimmer unpubl. data). Two horizontal, circular plates (60-cm diameter, 15 cm apart) formed the entrance region to the intake (center of upper plate, 1 mab). Beginning a few centimeters from the edge, the plates tapered at a 30° angle, thus forming a very thin rim. Water was pumped up into the intake, covered by 1-mm prefilter, and then along a channel spanned at its terminus by a $100\text{-}\mu\text{m}$ -mesh strip. Volume flux (0.4 L s^{-1}) at the intake was not sufficient to resuspend sediments (Ma and Grassle 2004). Larvae retained on the mesh were covered with another $100\text{-}\mu\text{m}$

mesh strip and wound onto a take-up spool submerged in 4% buffered formalin with rose bengal stain. Samples were later transferred to 80% buffered ethanol.

During each 24-h collection interval, water (nominally 100 L) was pumped for a preset interval of 5 min at the beginning of each hour (24 samples per deployment). Exact volume of each collection was recorded by the pump computer after sampling. Autocorrelations were done for each taxon and date. When needed, data were detrended to remove first-order effects. Correlations were run between larval concentrations and hour of day. Cross correlations (current speed and larval concentration) assessed relationships between variables at different time lags.

Sample processing—All polychaete individuals were enumerated from samples. This taxon historically comprised 40–80% of the infauna at Sta. 35 (Sanders et al. 1980; Butman 1989). Here, we focused almost exclusively on the two most abundant species, *Mediomastus ambiseta* (hereafter *Mediomastus*) and *Sabellaria vulgaris* (hereafter *Sabellaria*). Each individual was categorized by life stage using descriptions from the literature (Vannucci 1960; Eckelbarger 1975; Bhaud and Cazaux 1987). *Mediomastus* stages were based on number of setigers: larvae (≤ 11), juveniles (12–30), and adults (> 30). *Sabellaria* larvae have fewer than six setigers, and are distinctive morphologically (spatulate setae on the third setiger, plumb bodies, setae fanned out). Older stages were divided into two size classes: juveniles ($\leq 2.7 \text{ mm}$) and adults ($> 2.7 \text{ mm}$). Densities in floc (60 mL) and pump (100 L) samples were converted to number per cubic meter. Tray and core collections were normalized to sampled sediment volume (157 cm^3) for comparison with floc and pump data. All percentages are means for the three replicate dates, unless indicated otherwise.

Table 1. Percentages of the three life stages—larvae, juveniles, and adults—present in core, tray, and flocc samples for *Mediomastus ambiseta* and *Sabellaria vulgaris*. Values are given for each of the three sampling dates (cores and floccs) and intervals (trays), and for the mean of the dates.

Life stage	Cores (%)				Trays (mud+sand) (%)				Floccs (%)			
	24 Aug	31 Aug	06 Sep	Mean (%)	23–24 Aug	30–31 Aug	06–07 Sep	Mean (%)	24 Aug	31 Aug	07 Sep	Mean (%)
<i>Mediomastus ambiseta</i>												
Larvae	13.3	9.6	3.6	8.8	4.0	12.5	8.9	8.5	22.2	62.5	33.8	39.5
Juveniles	70.5	65.1	76.4	70.7	88.8	70.0	81.3	80.0	77.8	37.5	62.5	59.3
Adults	16.2	25.3	20.0	20.5	7.2	17.5	9.8	11.5	0	0	3.7	1.2
<i>Sabellaria vulgaris</i>												
Larvae									8.3	0	0	0.3
Juveniles									91.7	75.9	76.6	81.4
Adults									0	24.1	23.4	15.8

Results

Flow regime—Time series of 10-min averaged (low-passed) currents reflected a mixed, semidiurnal tidal flow (M_2 of 12.42 h) (Fig. 1). Maximal velocities of the major axis current were 10–15 cm s⁻¹, oriented 21°E, nearly coincident with the principal axis of the upper bay. During larval deployments (late August and early September), tidal flows were faster during ebb than flood, but of similar duration. Near-bottom (1 mab, pump sensor) temperature varied between 19.5°C and 20.0°C. Thus, the three deployment intervals (23–24 August, 30–31 August, and 06–07 September) shared similar physical characteristics in terms of tidal flow and temperature.

Sediment trays—Colonization of trays was highly variable spatially. The most abundant species with planktonic larvae were *Mediomastus ambiseta* (subsurface deposit feeder) and *Prionospio* spp. (surface deposit feeders), with mean densities of 1.4×10^3 and 2.2×10^2 m⁻³, respectively. These taxa made up 60.7% and 10.2% of total polychaetes in trays, respectively. Over all dates, *Mediomastus* colonists were dominated by juveniles (80.0%), then adults (11.5%), and larvae (8.5%) (Table 1). Mean (\pm SE) sizes (number of setigers) of larvae + juveniles were 14.1 ± 0.13 (23–24 August, $n = 116$), 14.1 ± 0.42 (30–31 August, $n = 33$), and 13.0 ± 0.10 (06–07 September, $n = 102$), for a grand mean of 13.7 ± 0.37 ($n = 3$). Juvenile size thus was similar among dates, despite differences in settlement densities. Adult presence in trays is somewhat puzzling. The cups prevented immigration by lateral burrowing, so adults either crawled on the surface or were passively transported into the cups. *Sabellaria vulgaris*, a reef-building suspension feeder that constructs tubes from coarse sand, occurred rarely (one in sand and five in mud over all dates; all juveniles) in the trays.

Mediomastus and *Prionospio* spp. showed consistent, often strong, sediment affinity. Mean total density was much higher in mud than sand, but none of the paired comparisons were statistically significant due to high variances (Fig. 2; Table 2). A power analysis was conducted to determine the number of replicates needed for an 80% probability of detecting a difference between the treatment (mud and sand) means. For $\alpha = 5\%$, $\beta = 20\%$, and using six pairs of means and variances (Fig. 2), 45 (median; 42.1 mean) replicates would be needed to show a difference between the two treatments. These results underscore the extreme patchiness in settlement at this site. The replication required to detect a significant difference between settlement in mud or sand would be intractable, except perhaps during periods of highest settlement, such as 23–24 August when $N = 8$ replicates might have been sufficient.

In cores, *Mediomastus* and *Prionospio* spp. were, again, the most abundant species (77.8% and 19.2% of ambient polychaetes) with mean densities of 3.5×10^4 and 1.0×10^4 m⁻³, respectively. Juveniles (70.4%) were the dominant stage class of recruits (Table 1). The percentage of adult *Mediomastus* in cores (20.5) was higher than in trays (11.4). Size (number of setigers) of larvae + juveniles was 17.5 ± 3.10 (grand mean, $n = 2$; no size data for 23–24 August),

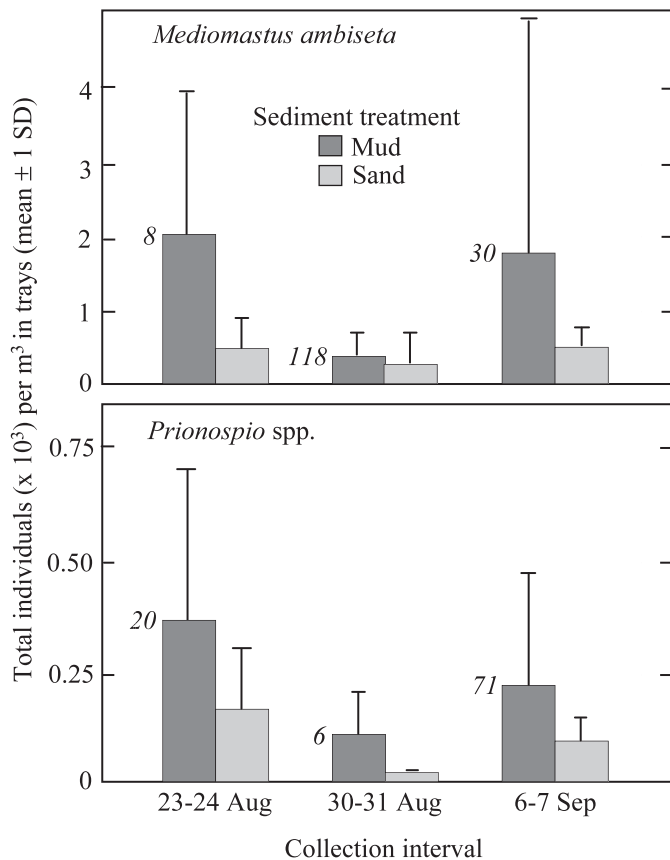


Fig. 2. Total individuals for the two most abundant polychaete taxa recovered from trays containing ambient mud or sand, and deployed for three 24-h intervals. There were three replicate trays per treatment and values are normalized to tray surface area (78.5 cm²). Given the low replication and high variability within treatments, a power analysis was conducted (see text). The bold, italicized number to the left of each treatment pair indicates the number of replicates required to show a significant difference between the mud and sand means.

~ 4 setigers larger than in trays. This last result would be expected for an established benthic population.

Floc—Floc samples contained very high densities of *Mediomastus* (mean of $1.7 \times 10^5 \text{ m}^{-3}$) and *Sabellaria* $4.3 \times 10^5 \text{ m}^{-3}$ (Fig. 3). These values exceeded, by 2–3 orders of magnitude, mean densities of *Mediomastus* in tray ($1.4 \times 10^3 \text{ m}^{-3}$) and *Sabellaria* in pump ($3.3 \times 10^2 \text{ m}^{-3}$, see next section) samples. All worms were in excellent condition. *Sabellaria* made up a larger proportion (52.4%) of the polychaete fauna than did *Mediomastus* (20.7%). For *Sabellaria*, juveniles (81.4%) dominated flocs, followed by adults (15.8%) and rare (0.3%) larvae (Table 1). Relative to *Sabellaria*, there were fewer (59.3%) *Mediomastus* juveniles, more (39.5%) larvae, and rare (1.2%) adults in flocs (Table 1). Mean (\pm SE) sizes (number of setigers) of *Mediomastus* larvae + juveniles were 16.3 ± 0.71 (24 August, $n = 27$), 16.25 ± 1.36 (31 August, $n = 24$), and 16.70 ± 0.62 (7 September, $n = 77$), for a grand mean of 16.42 ± 0.14 ($n = 3$). Larvae + juveniles collected in flocs were larger, on average, than they were in trays, perhaps

Table 2. Two-way (sediment treatment, collection interval) analyses of variance run separately for settlement of *Mediomastus ambiseta* and *Prionospio* spp. in trays (see Fig. 2).

Factor	SS	df	MS	F	p
<i>Mediomastus ambiseta</i>					
Sediment treatment	1184.22	1	1184.22	2.06	0.17
Collection interval	734.33	2	367.16	0.64	0.54
Treatment \times interval	510.78	2	255.39	0.44	0.65
Error	6896.67	12	574.72		
<i>Prionospio</i> spp.					
Sediment treatment	16.05	1	16.05	1.82	0.20
Collection interval	31.44	2	15.72	1.78	0.21
Treatment \times interval	2.78	2	1.39	0.16	0.86
Error	106.00	12	8.83		

reflecting an extended growth period afforded by the suspended aggregates.

Plankton pump—Spionids were the most numerous larvae collected during all three intervals (83.7% of total polychaetes, all three dates), but they could not be identified to species. *Sabellaria vulgaris*, the next most abundant taxon (15.1% of total polychaetes), was collected as late-stage larvae (4–5 setigers), approaching settlement size (6 setigers, Eckelbarger 1975).

Mediomastus, the most abundant settler at the site, was curiously and inexplicably absent from the pump samples, even though larvae settled and metamorphosed in the trays and flocs. The larvae are ~ 250 μm at settlement stage (Grassle and Grassle 1984), and therefore would not slip through the pump mesh. A satisfactory explanation is lacking for this conundrum.

Larval concentration time series were highly variable, especially for 23–24 August when densities in sequential 1-h samples sometimes fluctuated by a factor of 10 or more (e.g., Fig. 4B for *Sabellaria*). Positive autocorrelation was significant ($p < 0.05$) only at lag 1 for log-transformed *Sabellaria* densities during all three collection intervals, reflecting rapid decay in high larval densities and the spiky nature of the time series.

Two factors that may affect temporal variation in larval concentrations are time of day (larval vertical migration) and flow speed (passive transport). Log-larval *Sabellaria* density vs. hour of the day (all dates combined and each date separately) resulted in concave curves, with peak values around noon and lowest values around midnight. This diurnal pattern may result from active vertical migration within near-bottom waters. Larvae may move up (above pump depth) in the evening and down (to pump height) at midday, perhaps to avoid visual predators (Garland et al. 2002). Horizontal transport potentially could redistribute larvae, but cross correlations between *Sabellaria* concentration and flow speed were not significant at any lag.

Discussion

Larval supply failed to forecast settlement in muddy, coastal sediments. Copious *Sabellaria* larvae near the bed

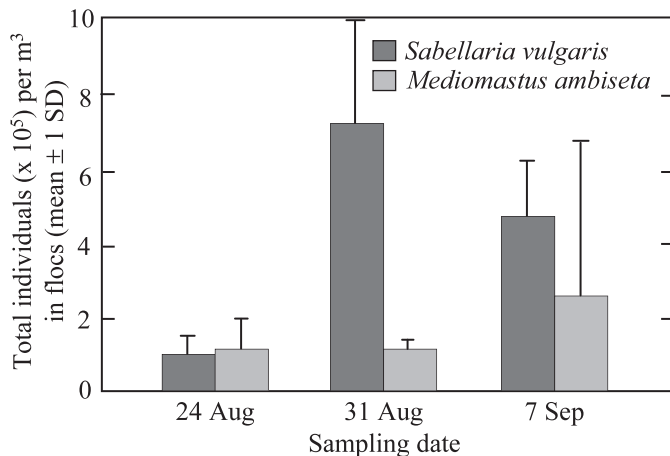


Fig. 3. Total individuals of *Sabellaria vulgaris* and *Mediomastus ambiseta* in near-bed flocculated particulates collected just prior to retrieval of the trays. Values are normalized to sample volume (60 mL).

did not predict their virtual absence in trays, and the paucity of planktonic *Mediomastus* larvae did not portend their high densities in trays. These parameters were decoupled due to high temporal variation in larval availability and high spatial variation in the colonization of trays.

Proposed mechanisms responsible for these results are hydrodynamically generated larval patches that transport and can touch down, together with flocs that could transport and deposit the settlers (Zimmer et al. 2008). Here, flocs contained more individuals than any other sample type, and may well serve as a medial, potentially productive, habitat between the water column and seafloor. *Mediomastus* larvae + juveniles were, on average, smallest in trays (13.7 setigers), intermediate in flocs (16.4 setigers), and largest in cores (17.5 setigers), suggesting that the floc environment confers more growth (like the natural bottom) than the defaunated sediment in trays. Likewise, the very large percentage of juveniles (81.4%) and 15.8% adult *Sabellaria* in flocs suggests that these worms were not simply colonizing flocs; they were living and growing in them. Flocs could be a decoupling agent on short time scales. Supply did not predict *Sabellaria* densities in flocs, and *Mediomastus* abundances in flocs did not forecast tray collections (Fig. 4). At equilibrium, flocs may supply a local habitat with suitable settlers, but transient planktonic densities (measured here) in near-bed waters, trays of sediment, and ambient cores are *unlikely* to reflect steady state.

Hydrodynamic considerations—At the scales sampled herein, hydrodynamic processes could contribute to the decoupling of supply and settlement. Both remote and proximal physical mechanisms could create larval patchiness in the plankton. At large scales (tens to hundreds of kilometers), numerical modeling has shown that wind-generated coastal eddies entrain (fish) larvae, forming temporally persistent patches (Siegel et al. 2008). Larval settlement would result from chance encounters of eddy-

generated packets of settlers with suitable substrate. Local processes, however, would determine supply and settlement in Buzzards Bay, especially within the array.

In the bay, residual currents result from nonlinearity in the dynamics of the tidal flow (Geyer and Signell 1992). Rectified mean, low-passed tidal currents produce residual eddies (of order 2–5 km) that potentially retain larval patches. When such eddies are comparable in size to the tidal excursion length scale, as in Buzzards Bay (4 km), larvae would be dispersed during transport by the rectilinear currents. This mechanism can be the dominant diffusive process in regions with strong tidal rectification, but perhaps not at Sta. 35. The magnitude of low-frequency dispersion scales with tidal velocity, which is stronger at the mouth than at the head of the bay. Moreover, recent three-dimensional modeling of hydrodynamics in Buzzards Bay (Sankaranarayanan 2007) indicates that tide-induced residual currents (and potentially dispersion) are much smaller than predicted by Signell (1987).

Additional processes may have determined spatially variable settlement in the trays. Episodic turbulent fluctuations in the bottom boundary-layer flow deliver larvae to the bed and determine the probability of anchoring (Crimaldi et al. 2002). Temporal fluctuations in larval settlement may bear the erratic signature of a bed stress time series. Near-bed larval densities in this study were indeed spiky, varying by up to an order of magnitude between hourly collections. Instantaneous settlement likely reflects this intermittent turbulence. Settlement was integrated, however, over each 24-h interval for comparison to daily collection intervals. Yet, despite the smoothing of the spiky hourly samples, larval supply did not predict daily settlement.

In summary, hydrodynamically generated larval patchiness, from eddy packets at large scales in the plankton to erratic bed stresses at much smaller scales on the bed, potentially could contribute to observed decoupling between supply and settlement. In addition, a discontinuous layer of benthic aggregates may inadvertently facilitate near-bed transport and site selection by competent settlers, and in the process, enhance system-wide temporal and spatial variability.

Role of benthic flocs in larval transport and site selection—Aggregated particulates are created throughout the water column by Brownian motion, shear, and differential sedimentation (McCave 1984), and within the bottom boundary layer due to large shears and associated mixing (Hill 1998). When bottom shear stresses are small, aggregates settle as flocs on the bed. Because flocs are less dense than most sediment, they are vulnerable to transport by even very slow flows. Compositionally diverse, aggregates are often rich in sticky mucopolysaccharides released by phytoplankton, bacteria, and suspension-feeding bivalves (Heinonen et al. 2007). As in pelagic aggregates, benthic flocs are rich in labile organics supporting diverse microbial communities readily consumed by benthic invertebrates (Simon et al. 2002). Thus, flocs offer settling larvae a physical matrix, sticky surfaces, and a veritable feast of organics and microbial prey.

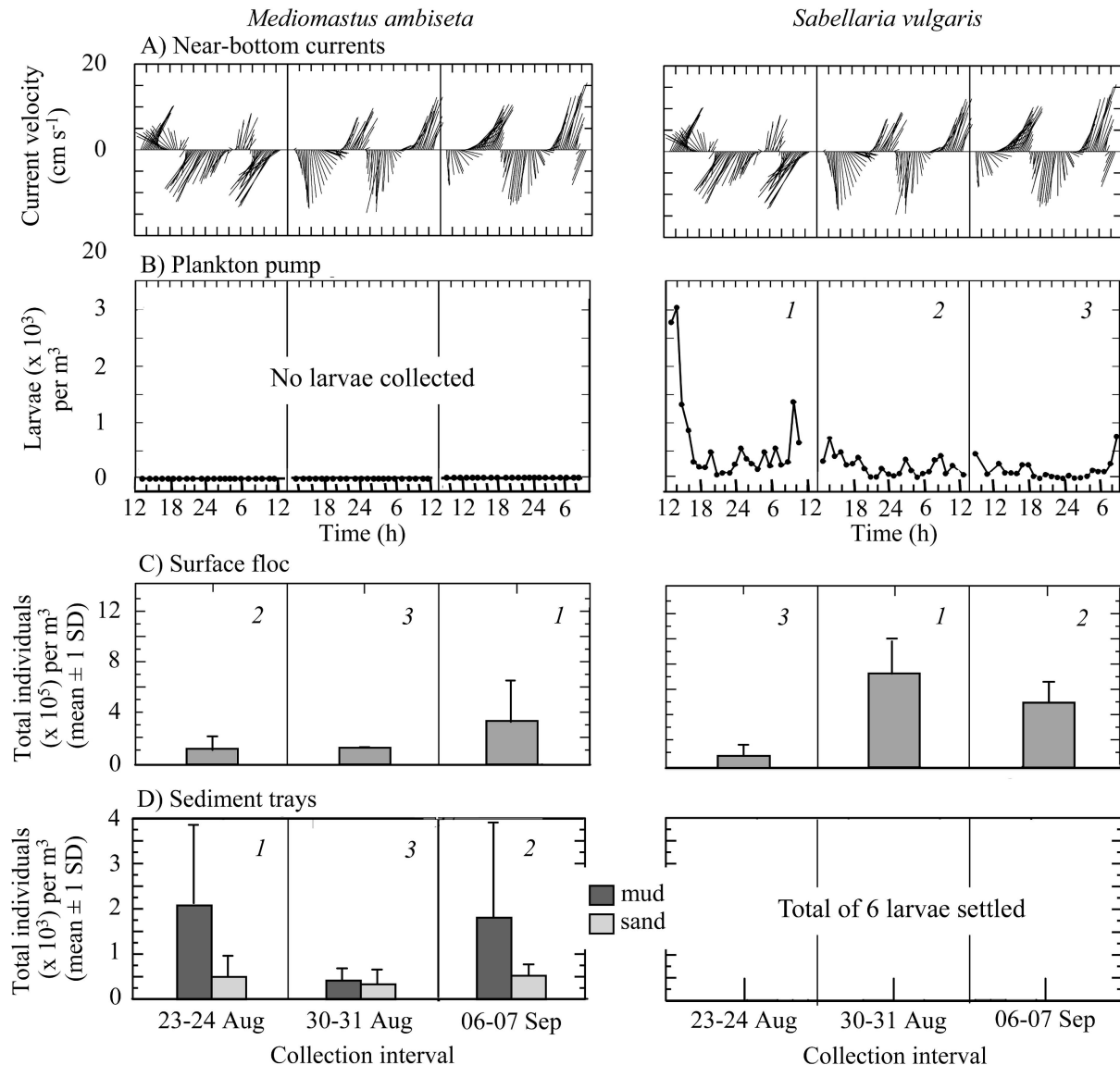


Fig. 4. Composite of all data collected for *Mediomastus ambiseta* (left) and *Sabellaria vulgaris* (right), including (A) near-bottom currents (Fig. 1), for reference, and collections by the (B) plankton pump, (C) surface flocs, and (D) sediment trays during the three collection intervals. The rank order of collection intervals for *Sabellaria* pump and floc data and for *Mediomastus* floc and tray data are indicated by the italic number in the top right-hand corner of each graph.

High densities (of order 10^3 m^{-3}) of larvae and juveniles previously were measured in aggregates (“marine snow”) collected 3–5 m below the water surface (Shanks and Edmondson 1990). Marine snow sinks faster than most larvae, so it was proposed that competent individuals actively enter aggregates and “ride” them to the bottom. Likewise, drifting near-bed aggregates, sampled here, may function as a way station for potential settlers. As a dynamic intermediate venue (for competent larvae), between water column and seafloor, flocs may seed the bed with resident species, while retaining taxa that naturally reside elsewhere.

Whither in flocs—*Sabellaria* and *Mediomastus* were the two most abundant species in flocs. They were collected in

strikingly different relative abundances by the other samplers (Fig. 4). *Mediomastus*, a long-term inhabitant of Sta. 35 and muddy sediments throughout Buzzards Bay (Sanders et al. 1980; Butman 1989; Snelgrove 1994), was not collected by the pump but readily colonized the mud trays and recruited to the ambient bottom (cores). At this time of year, *Mediomastus* postlarvae were previously the most abundant settler in traps mounted ~ 1 m above bottom over 4 yr (Butman 1989). Like other capitellids, *Mediomastus* larvae would swim slowly (of order 1 mm s^{-1} , C.A. Butman et al. 1988), and could not actively avoid the pump intake.

In contrast, *Sabellaria* naturally lives in coarse sands, forming extensive reefs (Brown and Miller 2011). A few *Sabellaria* adults (Sanders et al. 1980) and larvae (Butman

1989) were collected previously at Sta. 35. In the present study, this species was very abundant in pump samples, rare in the trays, and absent from cores. Relative to life stage, both species were collected primarily (mean of 71.6%, Table 1) as juveniles by all samplers except the pump. *Mediomastus* juveniles were very young in core, tray, and floc (~ 50%) samples. In contrast, *Sabellaria* juveniles in flocs were 1–2 weeks old.

Proportions of the life stages of each species in flocs may implicate its role in settlement. The mixture of larvae and juveniles in flocs appears to be labile (larvae in, larvae + juveniles out) for *Mediomastus*, but not for *Sabellaria*. We propose that *Mediomastus* larvae (39.4%) colonized near-bed aggregates, where they fed (or not), metamorphosed into juveniles (59.3%), and ultimately exited via settlement onto suitable, ambient substrate. Larvae could settle directly onto the bed or settle from flocs onto the bottom. *Mediomastus* exodus from floc, presumably to colonize hospitable habitat, is reflected by the small percentage (1.2%) of adults remaining in flocs. *Sabellaria* larvae also presumably entered flocs as larvae (given high larval availability as indicated by pump samples), fed (or not), and metamorphosed. In the absence of a suitable substrate, however, juveniles (81.4%) remained in aggregates and grew, with 15.8% reaching adulthood.

A variable last lap—Remote (eddy diffusion) and proximal (bed stress) physical processes could have contributed to observed decoupling of larval supply and settlement. Although hydrodynamics can play a major role in transporting, mixing, and depositing larvae, it is only one part of this story. An additional proposed mechanism involves flocs rolling along the bed, incidentally collecting larvae from near-bed plankton, and facilitating site selection. This mechanism may introduce previously uncharted variability into both supply and settlement. The process would operate only where near-bed aggregates are generated (coastal embayments, estuaries, kelp beds) or where they sink as marine snow from above. Which types of flocs entrain or transport larvae remain to be seen. As a near-bottom depot for the last leg of a larva's planktonic journey, flocs form a provocative link between water column and seafloor.

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References

BHAUD, M., AND C. CAZAUX. 1987. Description and identification of polychaete larvae; their implications in current biological problems. *Oceanis* (Paris), v. 13, part 6. Institut Oceanographique.

- BROWN, J. R., AND D. C. MILLER. 2011. Persistence and distribution of temperate intertidal worm reefs in Delaware Bay: A comparison of biological and physical factors. *Estuaries Coasts* **34**: 583–596, doi:10.1007/s12237-011-9387-5
- BUTMAN, B., R. SIGNELL, P. SHOUKIMAS, AND R. C. BEARDSLEY. 1988. Current observations in Buzzards Bay, 1982–1986. Open File Report 88-5. U.S. Geological Survey.
- BUTMAN, C. A. 1989. Sediment-trap experiments on the importance of hydrodynamical processes in distributing settling invertebrate larvae in near-bottom waters. *J. Exp. Mar. Biol. Ecol.* **134**: 7–88.
- , J. P. GRASSLE, AND E. J. BUSKEY. 1988. Horizontal swimming and gravitational sinking of *Capitella* sp. I (Annelida: Polychaeta) larvae: Implications for settlement. *Ophelia* **29**: 43–57.
- COWEN, R. K., AND S. SPONAUGLE. 2009. Larval dispersal and marine population connectivity. *Annu. Rev. Mar. Sci.* **1**: 443–466, doi:10.1146/annurev.marine.010908.163757
- CRIMALDI, J. P., J. K. THOMPSON, J. H. ROSMAN, R. J. LOWE, AND J. R. KOSEFF. 2002. Hydrodynamics of larval settlement: The influence of turbulent stress events at potential recruitment sites. *Limnol. Oceanogr.* **47**: 1137–1151, doi:10.4319/lo.2002.47.4.1137
- DOHERTY, K. W., AND C. A. BUTMAN. 1990. A time- or event-triggered automated, serial plankton pump sampler, p. 1–8. In D. Fry, E. Stone, and A. Martin [eds.], *Advanced Engineering Laboratory project summaries—1989*. Woods Hole Oceanographic Institution Technical Report 90-20. Woods Hole Oceanographic Institution.
- ECKELBARGER, K. J. 1975. Developmental studies of post-settling stages of *Sabellaria-vulgaris* (Polychaeta-Sabellariidae). *Mar. Biol.* **30**: 137–149, doi:10.1007/BF00391588
- GARLAND, E. D., C. A. ZIMMER, AND S. J. LENTZ. 2002. Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations. *Limnol. Oceanogr.* **47**: 803–817, doi:10.4319/lo.2002.47.3.0803
- GEYER, W. R., AND R. P. SIGNELL. 1992. A reassessment of the role of tidal dispersion in estuaries and bays. *Estuaries* **15**: 97–108, doi:10.2307/1352684
- GRASSLE, J. P., AND J. F. GRASSLE. 1984. The utility of studying the effects of pollutants on single species populations in benthos of mesocosms and coastal ecosystems, p. 621–642. In H. H. Harris [ed.], *Concepts in marine pollution measurements*. Maryland Sea Grant Publications.
- HEINONEN, K. B., J. E. WARD, AND B. A. HOLOHAN. 2007. Production of transparent exopolymer particles (TEP) by benthic suspension feeders in coastal systems. *J. Exp. Mar. Biol. Ecol.* **341**: 184–195, doi:10.1016/j.jembe.2006.09.019
- HILL, P. S. 1998. Controls on floc size in the sea. *Oceanography* **11**: 13–18.
- JENKINS, S. R. 2006. Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles. *J. Anim. Ecol.* **74**: 893–904, doi:10.1111/j.1365-2656.2005.00985.x
- LEVIN, L. A. 1990. A review of methods for labeling and tracking marine invertebrate larvae. *Ophelia* **32**: 115–144.
- MA, H., AND J. P. GRASSLE. 2004. Invertebrate larval availability during summer upwelling and downwelling on the inner continental shelf off New Jersey. *J. Mar. Res.* **62**: 837–865, doi:10.1357/0022240042880882
- MCCAVE, I. N. 1984. Size spectra and aggregation of suspended particles in the deep ocean. *Deep-Sea Res.* **31**: 329–352.
- NOWELL, A. R. M., AND P. A. JUMARS. 1984. Flow environments of aquatic benthos. *Annu. Rev. Ecol. Syst.* **15**: 303–328, doi:10.1146/annurev.es.15.110184.001511
- , AND ———. 1987. Flumes: Theoretical and experimental considerations for simulation of benthic environments. *Oceanogr. Mar. Biol. Annu. Rev.* **25**: 91–112.

- ÓLAFSSON, E. B., C. H. PETERSON, AND W. G. AMBROSE. 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments—the relative significance of presettlement and postsettlement processes. *Oceanogr. Mar. Biol. Annu. Rev.* **32**: 65–109.
- PECHENIK, J. A., M. S. ESTRELLA, AND K. HAMMER. 1996. Food limitation stimulates metamorphosis of competent larvae and alters post-metamorphic growth rate in the marine prosobranch gastropod *Crepidula fornicata*. *Mar. Biol.* **127**: 267–275, doi:10.1007/BF00942112
- PINEDA, J., F. PORRI, V. STARCZAK, AND J. BLYTHE. 2010. Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. *J. Exp. Mar. Biol. Ecol.* **392**: 9–21, doi:10.1016/j.jembe.2010.04.008
- SANDERS, H. L., J. F. GRASSLE, G. R. HAMPSON, L. S. MORSE, S. GARNER-PRICE, AND C. C. JONES. 1980. Anatomy of an oil spill: Long-term effects from the grounding of the barge Florida off West Falmouth, Massachusetts. *J. Mar. Res.* **38**: 265–380.
- SANKARANARAYANAN, S. 2007. Modeling the tide and wind-induced circulation in Buzzards Bay. *Estuar. Coast. Shelf Sci.* **73**: 467–480, doi:10.1016/j.ecss.2006.12.022
- SHANKS, A. L., AND E. W. EDMONDSON. 1990. The vertical flux of metazoans (holoplankton, meiofauna, and larval invertebrates) due to their association with marine snow. *Limnol. Oceanogr.* **35**: 455–463, doi:10.4319/lo.1990.35.2.0455
- SIEGEL, D. A., S. MITARAI, C. J. COSTELLO, S. D. GAINES, B. E. KENDALL, R. R. WARNER, AND K. B. WINTERS. 2008. The stochastic nature of larval connectivity among nearshore marine populations. *Proc. Natl. Acad. Sci. USA* **105**: 8974–8979, doi:10.1073/pnas.0802544105
- SIGNELL, R. P. 1987. Tide- and wind-forced currents in Buzzards Bay, Massachusetts. Woods Hole Oceanographic Institution Technical Report 87-15. Woods Hole Oceanographic Institution.
- SIMON, M., H. P. GROSSART, B. SCHWEITZER, AND H. PLOUGH. 2002. Microbial ecology of organic aggregates in aquatic ecosystems. *Aquat. Microbiol. Ecol.* **28**: 175–211, doi:10.3354/ame028175
- SNELGROVE, P. V. R. 1994. Hydrodynamic enhancement of invertebrate larval settlement in microdepositional environments: Colonization tray experiments in a muddy habitat. *J. Exp. Mar. Biol. Ecol.* **176**: 149–166, doi:10.1016/0022-0981(94)90182-1
- TAMBURRI, M. N., AND R. K. ZIMMER-FAUST. 1996. Suspension feeding: Basic mechanisms controlling recognition and ingestion of larvae. *Limnol. Oceanogr.* **41**: 1188–1197, doi:10.4319/lo.1996.41.6.1188
- VANNUCCI, M. 1960. Catalogue of marine larvae. Universidade de São Paulo, Instituto Oceanográfico.
- WIEBE, P. H., AND OTHERS. 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar. Biol.* **87**: 313–323, doi:10.1007/BF00397811
- ZIMMER, C. A., V. R. STARCZAK, V. S. ARCH, AND R. K. ZIMMER. 2008. Larval settlement in flocculated particulates. *J. Mar. Res.* **66**: 275–297, doi:10.1357/002224008785837167
- ZIMMER, R. K., J. T. FINGERUT, AND C. A. ZIMMER. 2009. Dispersal pathways, seed rains and the dynamics of larval behavior. *Ecology* **90**: 1933–1947, doi:10.1890/08-0786.1
- , AND C. A. ZIMMER. 2008. Dynamic scaling in chemical ecology. *J. Chem. Ecol.* **38**: 822–836, doi:10.1007/s10886-008-9486-3
- ZIMMERMAN, K. M., AND J. A. PECHENIK. 1991. How do temperature and salinity affect relative rates of growth, morphological-differentiation and time to metamorphic competence in larvae of the marine gastropod *Crepidula plana*? *Biol. Bull.* **180**: 372–386, doi:10.2307/1542338

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